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Estimating demographic contributions to effective population size in an age-structured wild population experiencing environmental and demographic stochasticity

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Abstract

1. A population's effective size (N_e) is a key parameter that shapes rates of inbreeding and loss of genetic diversity, thereby influencing evolutionary processes and population viability. However, estimating N_e , and identifying key demographic mechanisms that underlie the N_e to census population size (N) ratio, remains challenging, especially for small populations with overlapping generations and substantial environmental and demographic stochasticity and hence dynamic age-structure.
2. A sophisticated demographic method of estimating N_e/N , which uses Fisher's reproductive value to account for dynamic age-structure, has been formulated. However, this method requires detailed individual- and population-level data on sex- and age-specific reproduction and survival, and has rarely been implemented.
3. Here, we use the reproductive value method and detailed demographic data to estimate N_e/N for a small and apparently isolated red-billed chough (*Pyrrhocorax pyrrhocorax*) population of high conservation concern. We additionally calculated two single-sample molecular genetic estimates of N_e to corroborate the demographic estimate and examine evidence for unobserved immigration and gene flow.
4. The demographic estimate of N_e/N was 0.21, reflecting a high total demographic variance (σ_{dg}^2) of 0.71. Females and males made similar overall contributions to σ_{dg}^2 . However, contributions varied among sex-age classes, with greater contributions from 3 year-old females than males, but greater contributions from ≥ 5 year-old males than females.
5. The demographic estimate of N_e was ~ 30 , suggesting that rates of increase of inbreeding and loss of genetic variation per generation will be relatively high. Molecular genetic estimates of N_e computed from linkage disequilibrium and approximate Bayesian computation were approximately 50 and 30, respectively, providing no evidence of substantial unobserved immigration which could bias demographic estimates of N_e .
6. Our analyses identify key sex-age classes contributing to demographic variance and thus decreasing N_e/N in a small age-structured population inhabiting a variable environment. They thereby demonstrate how assessments of N_e can incorporate stochastic sex- and age-specific demography and elucidate key demographic

processes affecting a population's evolutionary trajectory and viability. Furthermore, our analyses show that N_e for the focal chough population is critically small, implying that management to re-establish genetic connectivity may be required to ensure population viability.

KEYWORDS

conservation genetics, evolutionary potential, iteroparity, life-history variation, population connectivity, population management, reproductive skew

1 | INTRODUCTION

A population's effective size, N_e , is a key parameter that shapes population-wide rates of inbreeding and loss of genetic diversity and, in combination with the strength of selection, determines mutation fixation probabilities (Charlesworth, 2009; Frankham, 1995; Nunney & Elam, 1994). Estimation of N_e , and elucidation of key underlying processes that cause the observed N_e , is therefore central in predicting evolutionary trajectories of finite populations (Charlesworth, 2009) and in evaluating population viability (Frankham, Bradshaw, & Brook, 2014; Mace & Lande, 1991), such that appropriate population management strategies can be devised (Hare et al., 2011; Laikre, Olsson, Jansson, Hössjer, & Ryman, 2016).

N_e is defined as the size of an idealized Wright-Fisher population that would experience the same rate of genetic drift as an observed population (Wright, 1931, 1969). Such a Wright-Fisher population is defined as a hypothetical population of constant finite size with no migration or selection and random mating between monoecious individuals in discrete generations, giving a Poisson distribution of reproductive success (Crow & Kimura, 1970; Wright, 1931). However, most natural populations violate key Wright-Fisher assumptions. Thus, N_e can exceed the census population size N (i.e. $N_e/N > 1$), up to a theoretical maximum of $2N$ given uniform reproductive success (Lande & Barrowclough, 1987; but see Waples, Luikart, Faulkner, & Tallmon, 2013). However, N_e is frequently smaller than N (i.e. $N_e/N < 1$), meaning that a population will experience greater genetic drift than expected given its N , potentially reducing its viability (Frankham, 1995; Nunney & Elam, 1994; Waples et al., 2013).

Many factors can reduce N_e below N , including varying N , skewed sex-ratio and high among-individual variance in reproductive success (i.e. high reproductive skew, Caballero, 1994; Frankham, 1995; Nomura, 2002; Ruzzante et al., 2016; Wright, 1931). Indeed, high variance in reproductive success is a dominant factor reducing N_e in diverse natural populations, spanning fish (e.g. red drum, *Sciaenops ocellatus*, Turner, Wares, & Gold, 2002; steelhead trout, *Oncorhynchus mykiss*, Araki, Waples, Ardren, Cooper, & Blouin, 2007), mammals (e.g. woodrats, *Neotoma macrotis*, Matocq, 2004) and amphibians (e.g. Italian agile frog, *Rana latastei*, Ficetola, Padoa-Schioppa, Wang, & Garner, 2010). Small populations (i.e. small N) can also experience substantial demographic stochasticity, which can exacerbate variance in reproductive success and further decrease N_e (Melbourne & Hastings, 2008; Palstra & Ruzzante, 2008). Consequently, at small N , N_e might

commonly be very small, further increasing genetic drift and threatening population viability.

Conversely, some studies have found an inverse relationship between N_e/N and N , implying that small populations have higher N_e than might be expected given their N (Ardren & Kapuscinski, 2003; Hedrick, 2005; Palstra & Ruzzante, 2008; Pray, Goodnight, Stevens, Schwartz, & Yan, 1996; Watts, Saccheri, Kemp, & Thompson, 2007). Such patterns can arise if the among-individual variance in reproductive success decreases at small N , for example because environmental stochasticity reduces the reproductive success of all population members, or because male-male competition for mates or breeding sites is reduced (so-called 'genetic compensation' mechanisms, Ardren & Kapuscinski, 2003; Beebe, 2009; Palstra & Ruzzante, 2008). Given the range of possible values and causes of N_e/N , pervasive aims across evolutionary, population and conservation ecology are to estimate N_e/N in diverse natural populations and identify the key contributing demographic processes, and thereby elucidate general relationships between N_e , N , and underlying demography and population dynamics (Frankham, 1995; Palstra & Fraser, 2012; Ruzzante et al., 2016; Waples et al., 2013).

For most natural populations, N_e cannot be measured directly and must be estimated using demographic or molecular genetic approaches. Demographic approaches estimate N_e as mathematical functions of causal demographic parameters and processes that generate contemporary N_e , such as the variance in lifetime reproductive success, breeder sex-ratio or fluctuations in N (Caballero, 1994; Lande & Barrowclough, 1987). These demographic approaches estimate the variance effective size N_{ev} (i.e. the sampling variance in allele frequencies per generation) and thereby quantify N_e for the offspring generation (Caballero, 1994; Kimura & Crow, 1963). Such methods are valuable because, beyond providing a point estimate of N_e , they directly identify key demographic processes that shape N_e . They can therefore inform population management strategies aiming to increase N_e and reduce future loss of genetic diversity (Nunney & Elam, 1994; Ruzzante et al., 2016). However, many demographic methods rely on strong simplifying assumptions, such as discrete generations with no age-structure, no density-dependence and constant N , which are typically violated in natural populations (Caballero, 1994; Hill, 1972; Nomura, 2002; Nunney, 1991). Even recent methods for estimating N_e in age-structured populations with overlapping generations still require strong assumptions, such as constant N and birth rate and hence stable age-structure (e.g. the 'AgeNe' method, Waples, Do, & Chopelet, 2011) and consequently do not incorporate effects of environmental

or demographic stochasticity or additional demographic heterogeneity that generate dynamic age-structure. However, since theory predicts that environmental and demographic stochasticity and heterogeneity could substantially affect N_e , especially at small N , such effects should be incorporated to avoid biased estimates of N_e (Engen, Lande, & Saether, 2005; Engen, Lande, Saether, & Festa-Bianchet, 2007).

Accordingly, Engen et al. (2005) and Engen, Lande, Saether, and Gienapp (2010) derived a novel demographic method that utilizes the concept of 'reproductive value' to relax the assumption of stable age-structure and thereby capture effects of environmental and demographic stochasticity and additional demographic heterogeneity on N_e . Conceptually, this method considers the mean and variance in the change in frequency of a rare selectively neutral allele at each time-step in a hypothetical heterozygote subpopulation, given observed patterns of age-specific demographic variance (Emigh & Pollak, 1979; Engen et al., 2005). Overlapping generations and age-structure in a variable environment are incorporated using Fisher's reproductive value (i.e. the contribution of an individual of a given age to population growth rate), which can be summed across individuals in all age classes to give the population's total reproductive value given its age-structure (Crow & Kimura, 1970; Engen, Lande, Saether, & Dobson, 2009; Fisher, 1958). Changes in total reproductive value can then be used to obtain an estimate of total population growth rate, and hence the rate of increase of a neutral allele, thereby generating an estimate of N_e that is not biased by dynamic age-structure (Crow & Kimura, 1970; Engen, Lande et al., 2007; Engen et al., 2010).

The total variance in individual contributions to population growth rate in a dynamically age-structured population stems from demographic and environmental variances in age- and sex-specific fecundity and survival which, in practice, can be defined and estimated as the variances within years and in means among years, respectively (Engen, Bakke, & Islam, 1998). The required variance components can be estimated using the distribution of individual reproductive values among individuals within and among years, which can be used to estimate the total population demographic variance, σ_{dg}^2 . The N_e/N ratio can then be estimated as:

$$\frac{N_e}{N} = \frac{1}{\sigma_{dg}^2 T} \quad (1)$$

where T is the generation time (Appendix S1; Engen et al., 2005).

This calculation is potentially very insightful but imposes challenging data demands, requiring individual-level information on realized sex- and age-specific reproductive success and survival alongside population-level mean rates. To date, it has only been implemented in a Siberian jay (*Perisoreus infaustus*) population (as a methodological example considering three age classes, Engen et al., 2010) and a house sparrow (*Passer domesticus*) metapopulation (considering two age classes, Stubberud et al., 2017) where genetic variation and inbreeding rates may be influenced by immigration rather than solely local demography (e.g. Baalsrud et al., 2014). Indeed, immigration can cause local N_e to approach that for the whole metapopulation, meaning that N_e/N is largely independent of local demography (Gilbert & Whitlock, 2015; Wang & Whitlock, 2003). Consequently, studies that

apply the 'reproductive value' estimator of N_e/N to isolated populations are required to identify key demographic processes that influence N_e/N given environmental and demographic stochasticity and heterogeneity, and resulting dynamic age-structure.

Since sufficient data to implement any demographic estimator of N_e/N are often unavailable, N_e is commonly instead estimated from molecular genetic data. Single-sample approaches, which require DNA sampling at one time-point, are most practical for species with long T and where historical samples are not available (Palstra & Ruzzante, 2008). Such estimators generally measure inbreeding effective size N_{ei} (i.e. the rate of change in heterozygosity) and therefore reflect N_e of the parental generation (Caballero, 1994; Crow & Denniston, 1988). Given varying N , N_{ei} is expected to lag behind changes in N by at least one generation (Hill, 1972; Kimura & Crow, 1963; Waples, 2005), and might therefore give somewhat misleading estimates of current N_e . Additionally, molecular genetic estimates of N_e are calculated from resultant effects of N_e on genetic variation, and hence do not typically elucidate the ecological and demographic processes that cause the estimated N_e (but see Wang, Brekke, Huchard, Knapp, & Cowlshaw, 2010). However, such estimators can capture the genetic effects of immigration, which may remain undetected based solely on observations of N and local demography (Baalsrud et al., 2014; Gilbert & Whitlock, 2015; Hare et al., 2011). Consequently, to generate overall mechanistic understanding of N_e/N and N_e and hence elucidate stochastic evolutionary processes and inform population management strategies, molecular genetic estimators of N_e need to be calculated alongside appropriate demographic estimators.

Accordingly, we used detailed individual-level and population-level demographic data, and molecular genetic data, to estimate N_e/N and N_e in a small and apparently isolated red-billed chough (*Pyrrhocorax pyrrhocorax* Linnaeus, hereafter 'chough') population of major conservation concern. We utilized the 'reproductive value' demographic estimator (Engen et al., 2005) to account for environmental and demographic stochasticity and heterogeneity and resulting dynamic age-structure, and thereby identified key sex- and age-specific components of demographic variance that contribute to N_e/N . We additionally computed two single-sample molecular genetic estimates of N_e to infer effects of any unobserved immigration. We thereby demonstrate how N_e can be estimated in dynamically age-structured populations, and identify key demographic processes underlying N_e , thus aiding our general understanding of evolutionary processes in finite populations and informing conservation strategy.

2 | MATERIALS AND METHODS

2.1 | Focal population

Choughs are of conservation concern in Europe and the United Kingdom due to substantial reductions in range and population size and resulting fragmented distribution (Eaton et al., 2015). Comprehensive censuses undertaken every 3–6 years since 1982 show that the island of Islay holds most (ca. 84%) of the remaining Scottish chough population, yet numbers on Islay have decreased from 78 breeding pairs

in 1986 to 46 pairs in 2014 (Finney & Jardine, 2003; Hayhow et al., 2015; Trask et al., 2016; Appendix S2). High neutral genetic differentiation with other British chough populations (Wenzel et al., 2012), and a lack of observed immigration, suggest that Islay's population is isolated. This isolation and small N imply that inbreeding and loss of genetic diversity may compromise population viability.

Islay's choughs form territorial, socially monogamous breeding pairs and nest in caves or farm buildings (Bignal, Bignal, & McCracken, 1997) with little extra-pair parentage (~5% chicks, Trask et al., 2016). Both sexes breed once per year starting from age 2–4 years and survive to breed in multiple years (maximum breeding age: 17 years), generating overlapping generations (Reid, Bignal, Bignal, McCracken, & Monaghan, 2004). Reproductive success and survival vary among ages, years, cohorts, and nest sites (Reid, Bignal, Bignal, McCracken, & Monaghan, 2003a, 2003b, 2006; Reid et al., 2004). Sub-adult and non-breeding individuals aged 1 year or older form flocks that occupy known locations, meaning that all non-breeders can be readily observed and censused (Bignal et al., 1997; Reid et al., 2006, 2008). First-year survival (fledging to age 1 year) for the 2007–2009 cohorts was particularly low (Reid et al., 2011), causing low subsequent recruitment into the breeding population. Demographic estimation of N_e/N that accounts for environmental and demographic stochasticity and demographic heterogeneity, and resulting dynamic age-structure, is therefore required.

2.2 | Demographic estimation of N_e

2.2.1 | Age-specific breeding success and survival

Demographic estimation of N_e using reproductive value to account for dynamic age-structure (e.g. Engen et al., 2005, 2010) requires estimates of mean population-level sex-specific demographic rates underlying the deterministic asymptotic population growth rate (λ), defined for a pre- or post-breeding census. The required rates comprise the sex-specific probabilities of attempting to breed at each age (c_i), age-specific breeding success given a breeding attempt (m_i), and juvenile and subsequent age-specific annual survival probabilities (P_i , Caswell, 2001; Reid et al., 2004), where i denotes a sex-age class. Such estimation of N_e also requires individual-level data on age-specific reproductive success defined as the realized number of offspring that survived to age 1 year (b) and realized annual survival (J) from samples of individual females and males in a sample of years (Engen et al., 2005, 2010). All notations are summarized in Appendix S1 (Table S1).

To estimate the required population- and individual-level demographic rates, a sample of accessible chough nest sites across Islay were visited each year during 1983–2014. The number of nestlings that survived to ca. 3 weeks post-hatch was recorded, and nestlings were marked with unique colour-ring combinations (Reid et al., 2003b, 2004). Adults breeding at nest sites across Islay were subsequently identified from their colour-rings, and sexes were assigned based on reproductive behaviour and relative size (Bignal et al., 1997). The annual breeding success of known-age individuals was thereby recorded. Colour-ringed adults and sub-adults were resighted across Islay during

May–June each year, allowing age-specific annual resighting probabilities and apparent survival probabilities to be estimated using capture-mark-recapture (CMR) models (Reid et al., 2003a, 2004).

Initial year-structured CMR models showed that annual resighting probabilities were typically less than one prior to 2004, but approached one subsequently due to increased resighting efficiency (estimate across 2004–2014 of 0.97 ± 0.02 SE, Appendix S1). We consequently focussed on live individuals and, of those breeding, whose offspring were ringed in 2004–2013, so that individual-level realized survival (J) and reproductive success (b) could be directly recorded. Separate age classes for individuals aged one to four, and a pooled terminal age-class for individuals aged 5 years or older, were defined (i.e. $k = 5$ age classes). This structure captures age-specific variation in key demographic rates while maintaining sufficient sample sizes within each sex-age class (Appendix S1).

Resightings of individuals in non-breeding flocks vs. at nest sites were used to estimate the mean probability of breeding (c_i) for each sex-age class. Non-breeding individuals typically paired and showed courtship behaviour within flocks, allowing sexes to be assigned. The mean number of fledglings produced given that breeding was attempted (m_i) was directly estimated from breeding records for each sex-age class. Constrained CMR models were fitted to estimate separate age-specific survival probabilities (P_i) for 1983–2003 and 2004–2014 while retaining full encounter histories of all ringed individuals and maximizing power to estimate P_i for 2004–2014. Initial analyses showed that models that contained three age classes, first-year (P_1 , fledging to age 1 year), second-year (P_2 , age one to age two) and adult (P_{ad} , all subsequent ages) were strongly supported, thereby setting P_i equal across all individuals aged 2 years or older (Appendix S1). This three age-class structure is consistent with previous detailed analyses of age-specific P_i in Islay's choughs (Reid et al., 2004). Females and males were pooled for CMR analyses because sexes of individuals that died before pairing were unknown, and because previous analyses showed that P_{ad} does not differ between the sexes (Reid et al., 2003b, 2004). Additionally, previous analyses showed no evidence of strong density dependence in mean breeding success, or in P_1 , P_2 or P_{ad} (Reid et al., 2003a, 2008).

2.2.2 | Population projection matrix

The asymptotic population growth rate (λ), stable age distribution (u_i) and reproductive values (v_i) were calculated from a $2k \times 2k$ two-sex Leslie matrix (L). The matrix comprised four submatrices, formulated for a birth-pulse population with pre-breeding census, which describe the contributions of females and males to female and male offspring (Appendix S1). Top row fecundity f_i terms were calculated as:

$$f_i = \frac{1}{2} q(c_i m_i P_1) \quad (2)$$

where q is the primary proportion of the focal sex and the factor of $1/2$ is the probability that a hypothetical recessive allele is transmitted to each offspring, given a hypothetical subpopulation of heterozygotes that only mate with dominant homozygotes (Engen et al., 2010).

Subdiagonal transition probabilities P_2 and P_{ad} were the probabilities of survival from one age-class to the next (Appendix S1). Standard matrix algebra was used to compute u_i and v_i from the right and left eigenvectors of l (Caswell, 2001), scaled so that $\sum u_i = 1$ and $\sum u_i v_i = 1$, and to compute the generation time, T , as the mean projected age of parents of new offspring. Contributions to λ from the female and male submatrices must be the same (Caswell, 2001; Engen et al., 2010; Mesterton-Gibbons, 1993). λ was therefore initially calculated as the real dominant eigenvalue of the female and male submatrices separately to check that these were approximately equal, and then computed for the full two-sex matrix.

2.2.3 | Estimating demographic variance

The total population demographic variance, σ_{dg}^2 , comprises the sum of the contributions to demographic variance from each sex-age class, σ_{dgi}^2 , weighted by the stable age distribution, u_i :

$$\sigma_{dg}^2 = \sum \sigma_{dgi}^2 u_i \quad (3)$$

To calculate each σ_{dgi}^2 , we first calculated the demographic variance component from each sex-age class in each year using the mean b and J of each sex-age class i in each year, the mean sum of the squared difference of each individual's b and J from its sex-age class mean (S_b^2 and S_J^2), and the mean sum of squares of the cross-products of b and J (S_{bj}) (Appendix S1, Engen et al., 2010). These calculations included all individual colour-ringed choughs alive in each year during 2004–2013 whose value of b could be quantified, either because they produced zero fledglings (i.e. $b = 0$) or because their fledglings were colour-ringed meaning that the number of 1-year old offspring alive in 2005–2014 was observed. Whether each focal colour-ringed individual was alive the following year (i.e. 2005–2014), and hence individual J , was also observed directly.

The expected contributions from females and males to demographic variance from the production of sons and daughters was then calculated, conditioned on b and J from the individuals and years sampled. The brood sex-ratio does not differ significantly from 1:1 in Islay's choughs, meaning that $q = 0.5$ (Appendix S3). The contributions to demographic variance from the production of sons and daughters were consequently assumed to be equal (Appendix S1). These expected contributions and the reproductive values, v_i , computed from l , were used to compute σ_{dgi}^2 for each sex-age-year class. Each σ_{dgi}^2 was then weighted by sample size (Engen et al., 2010). Finally, N_e/N was calculated from Equation 1, and N_e was then calculated by defining N as the total census population size which includes both adults and sub-adults. Full details of all calculations, underlying data and sample sizes are provided in Appendix S1.

Bootstrap confidence intervals (CIs) around estimates of demographic variance for each sex-age class (σ_{dgi}^2), the total demographic variance (σ_{dg}^2) and N_e/N were initially computed for the full five age-class model, using 10,000 bootstrap samples. However, CIs for variances can be downwardly biased when bootstrap samples are drawn from small sets of observations with skewed distributions, because

rare high values might not be sampled (Manly, 2007; Puth, Neuhauser, & Ruxton, 2015; Schenker, 1985). This is likely for b , because few individuals were observed for some sex-age-year classes, and while most breeding attempts produced zero 1-year olds, a minority produced 2–4. Indeed, bootstrap CIs for σ_{dg}^2 and N_e/N computed from the full five age-class model scarcely included the point estimate. Therefore, to adequately assess uncertainty around σ_{dg}^2 and N_e/N estimates, these quantities were re-estimated using a reduced model with three age classes (i.e. $k = 3$, ages 1, 2 and 3 years or older), thereby increasing sample sizes for adult sex-year classes. Bootstrap samples for realized survival (J) and breeding success (b) were jointly drawn (with replacement) at the level of individuals within years for each sex-age-year class. This sampling regime is necessary to maintain any covariance in b and J within individuals, and to capture stochastic variation among individuals within years, which generates the demographic stochasticity of interest (Engen et al., 2010, Appendix S1).

Capture-mark-recapture models were fitted in program MARK (White & Burnham, 1999). Other analyses were run in R v2.15.2 (R Development Core Team 2012), using package Popbio (Stubben & Milligan, 2007) for population projections.

2.3 | Molecular genetic estimation of N_e

2.3.1 | DNA sampling and genotyping

Since adult choughs moult during breeding, DNA was non-invasively sampled by collecting moulted feathers from nest sites visited during 2007–2014. This provided DNA samples from a mixed-age sample of adult individuals nesting across Islay. DNA was extracted from 3 to 5 mm clippings of the lower feather calamus, using standard ammonium acetate precipitation (Hogan, Cooke, Burridge, & Norman, 2008; Trask et al., 2016). All samples were genotyped at 13 microsatellite loci developed for choughs and polymorphic in the Islay population (Wenzel, Webster, Segelbacher, Reid, & Piertney, 2011, Appendix S4). However, one locus (Ppy-005) did not conform to Hardy-Weinberg equilibrium and hence was excluded from analyses (Appendix S4). Duplicate samples from the same individual were identified and excluded to ensure that N_e estimates were not downwardly biased (Appendix S4).

2.3.2 | Genetic estimators of N_e

The best-evaluated single-sample molecular genetic estimator of N_e utilizes linkage disequilibrium (LD), and measures associations between alleles at different neutral loci compared to expectations given random mating and binomial sampling (Hill, 1981). In isolated, finite populations with random mating, LD stems from genetic drift and can be used to estimate N_e (Hill, 1981). We implemented a single-sample LD estimator of N_e in NeEstimator v2.01 (Do et al., 2014; Waples & Do, 2008). To relax the assumption of random mating given the chough's mating system, a model that assumes random initial mating followed by lifelong monogamy (Waples, 2006) was used. Furthermore, since Hill's (1981) equations

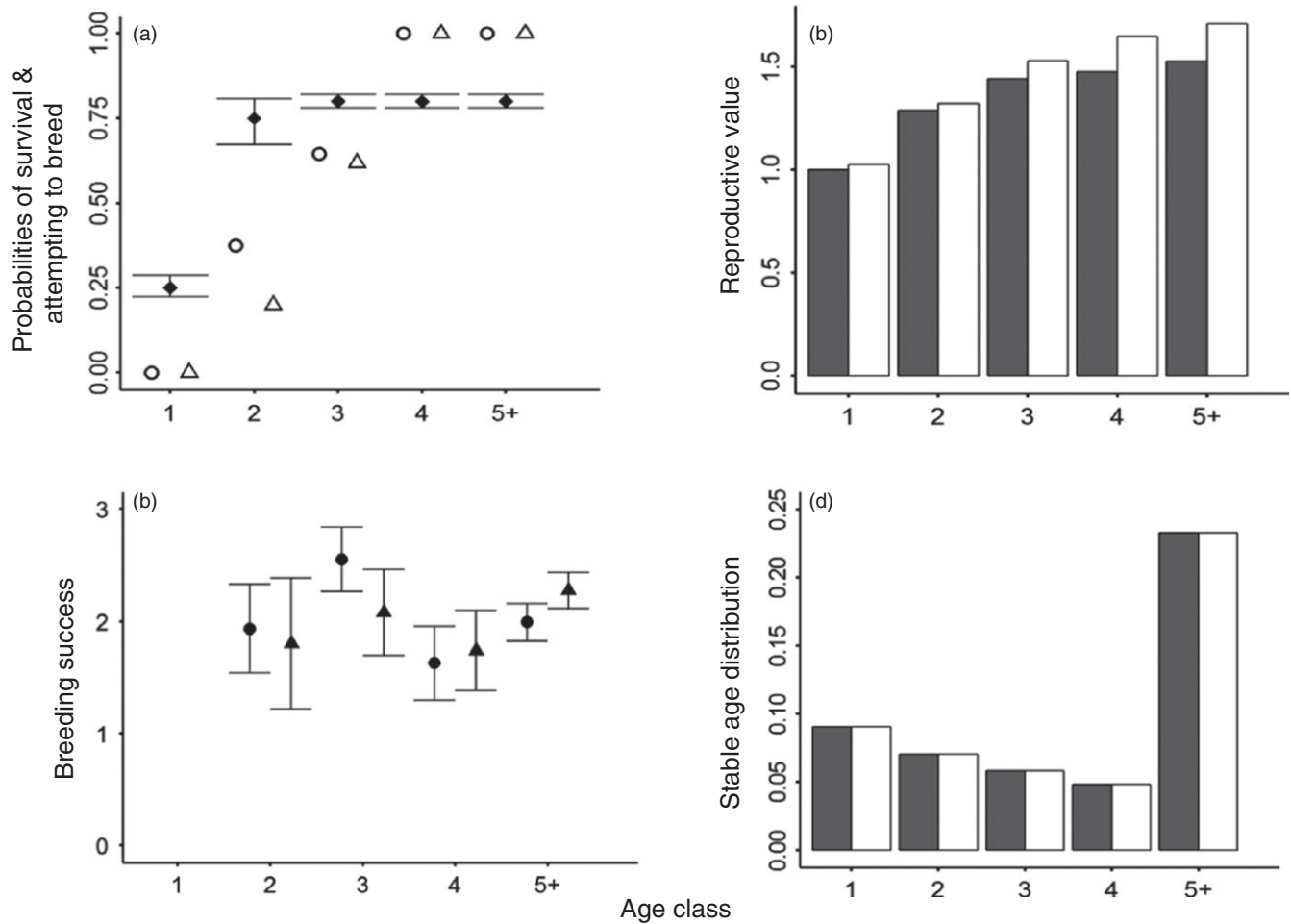


FIGURE 1 Age- and sex-class specific estimates of (a) annual survival probability (P_i , diamonds) with 95% confidence intervals, and probability of attempting to breed (c_i , grey filled symbols); (b) breeding success (number of fledglings produced) of individuals that attempted to breed (m_i), with associated standard errors; (c) reproductive values (v_i), and (d) stable age distribution (u_i). Females and males are, respectively, indicated by (a, b) circles and triangles, and (c, d) grey and white bars. Sample sizes are summarized in Table S2

can give downwardly biased estimates of N_e if the sample size is less than true N_e (England, Cornuet, Berthier, Tallmon, & Luikart, 2006), a bias-corrected analysis which adjusts for sample size was implemented (following Waples, 2006). Finally, since low frequency alleles can upwardly bias N_e estimates, alleles at frequency <0.02 were excluded (following Waples & Do, 2010). Sensitivity to such exclusions was examined by repeating analyses with exclusion thresholds of 0.01, 0.02 and 0.05. Although the LD method assumes discrete generations, it can give reasonably unbiased estimates of N_e for species with overlapping generations given genotypes from a mixed-age sample of adults, and if the number of cohorts represented roughly equals the generation length (Waples, Antao, & Luikart, 2014). These conditions are fulfilled by genotype data from adult choughs sampled during 2007–2014.

We additionally implemented an approximate Bayesian computation (ABC) single-sample estimator of N_e using program ONeSAMP (Tallmon, Koyuk, Luikart, & Beaumont, 2008), which compares eight summary statistics calculated from the focal population to the same statistics for 50,000 simulated populations with N_e drawn from within

specified lower and upper prior boundaries. Two different priors were specified; 2–180, with the upper prior reflecting the theoretical maximum N_e of $2N$, and 2–100, as N_e is generally lower than $2N$ in wild populations (Frankham, 1995; Nunney & Elam, 1994). Since single-sample genetic estimators of N_e utilize sampled breeding adults, N was taken as the total number of breeding adults in the population (Palstra & Fraser, 2012). As the eight ONeSAMP summary statistics may be differently affected by N_e of previous generations (Wang, 2009) and priors were defined by current N , genotype data from adults sampled during 2012–2014 were used.

3 | RESULTS

3.1 | Mean demographic rates and projection matrix

One year-old choughs never attempted to breed, and the probability of breeding (c_i) increased to one in individuals aged 4 years or older in both sexes (Figure 1a, Appendix S1). Across sampled individuals that attempted to breed, mean breeding success (m_i) increased from age

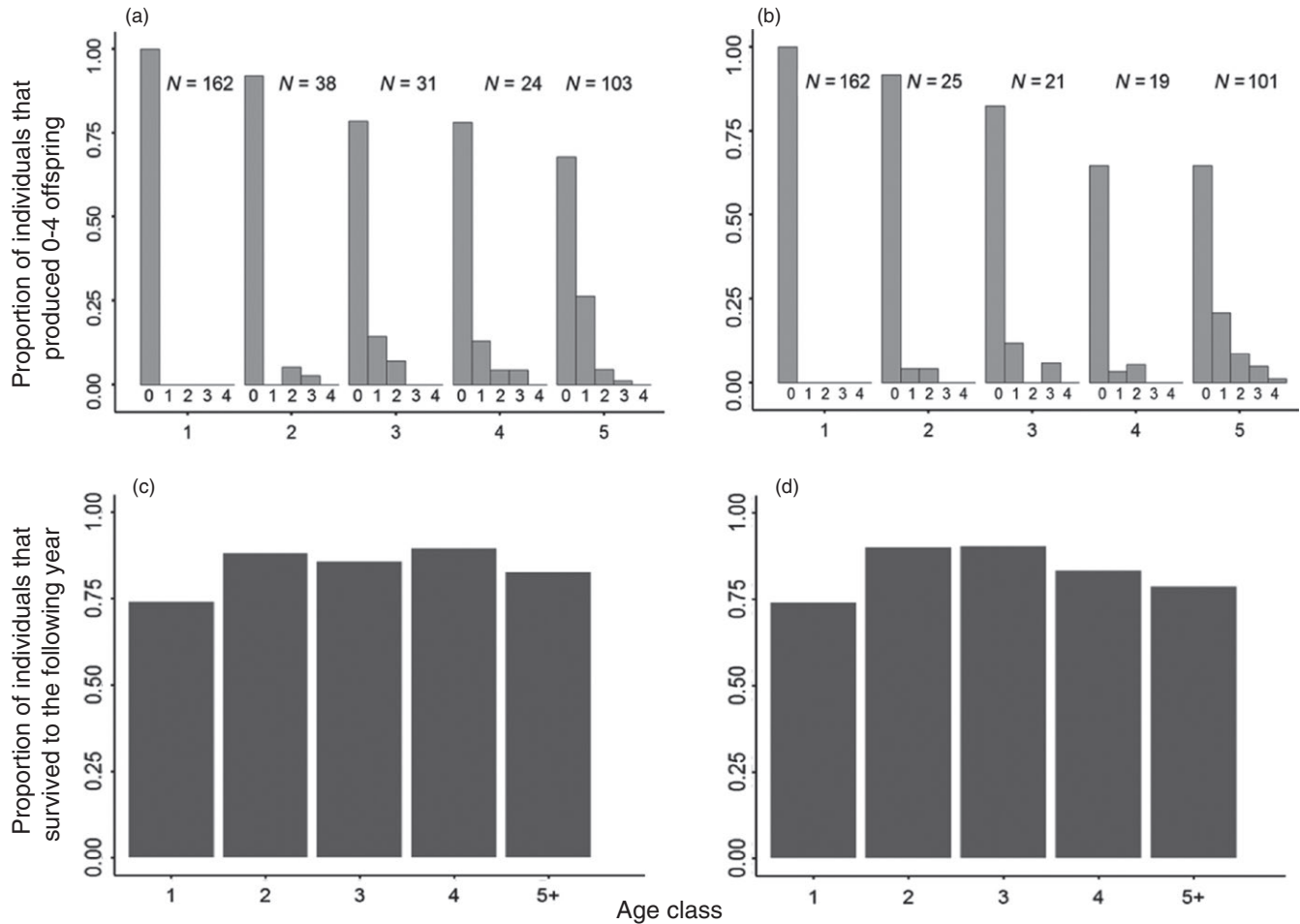


FIGURE 2 Proportions of (a) females and (b) males in each age-class that produced 0-4 1-year-old offspring (b), and (c) females and (d) males in each age-class that survived to the following year (J). On panels (a) and (b), the interior x-axes show the b values and exterior x-axes show the breeder age classes, where '5' includes individuals aged ≥ 5 years. N values denote sex-age specific sample sizes except for age one where sexes were unknown and hence N denotes the pooled sample size. J is consequently assumed to be equal for 1-year-old females and males (c, d)

two to three, and tended to be lower in 4-year-olds and higher again in individuals aged 5 years and older (Figure 1b, Appendix S1). Mean annual survival probabilities (P_i) increased from first-year through second-year to adult (Figure 1a, Appendix S1).

Consequently, reproductive values, v_i , increased with age and were slightly higher for males than for females in all age-classes (Figure 1c, Appendix S1). As expected, the proportional representation of age-classes measured by the stable age distribution values, u_i , decreased across initial age classes but was greatest for the pooled ≥ 5 age-class. Age-specific u_i values were equal for females and males because values of P_i were set equal (Figure 1a,d, Appendix S1). Population growth rate was approximately equal for the male and female submatrices ($\lambda_{\text{fem}} = 0.964$, $\lambda_{\text{male}} = 0.967$), so that for the two-sex matrix $\lambda = 0.965$ and generation time $T = 6.7$ years.

3.2 | Sex-age-year specific demographic rates

Reproductive success (b_i), calculated as the number of 1 year-olds produced per individual per year, varied among sex-age-year classes (Figure 2a, Appendix S1). Median b_i was zero in all sex-age classes,

but higher values occurred most frequently in females and males aged 5 years or older (Figure 2a,b). Realized survival (J_i) also varied among sex-age-year classes; as expected given the estimated P_2 and P_{ad} , fewer 1 year-olds survived to age two than survived through older ages (Figure 2c,d, Appendix S1). There was no consistently positive or negative covariance between J and b across individuals within each year (grand mean covariance = 0.04, Appendix S1).

3.3 | Demographic estimate of N_e

Given the two-sex five-age class model, $N_e/N = 0.21$ and $\sigma_{dg}^2 = 0.71$ (Figure 3, Appendix S1). Given the 2014 census of $N = 141$ choughs (including adults and sub-adults) and generation time $T = 6.7$ years, then $N_e = 30$. The reduced three-age class model returned only small changes in the point estimates, with fairly tight 95% bootstrap CIs ($N_e/N = 0.23$, 95% CI: 0.21–0.29; $\sigma_{dg}^2 = 0.67$, 95% CI: 0.53–0.75, Appendix S1).

The contribution to total σ_{dg}^2 varied among sex-age classes, such that older age classes contributed more than younger age classes (Figure 3). For 1-, 2- and 4-year-olds the estimated components of

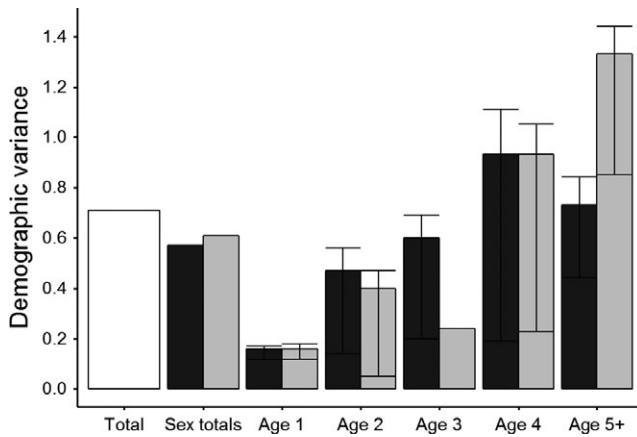


FIGURE 3 Total population demographic variance (σ_{dg}^2 , 'Total'), sex-specific components of σ_{dg}^2 ('Sex totals') and contributions to σ_{dg}^2 from each sex-age class (Age 1–5+ years). Dark grey and light grey bars indicate female and male components, respectively. Whiskers denote 95% bootstrapped confidence intervals. Bootstrap confidence intervals did not include the point estimate for 3-year-old males and are not shown (see Appendix S1)

σ_{dg}^2 were similar for females and males. However, 3-year-old females contributed more than 3-year-old males to σ_{dg}^2 (Figure 3). This pattern was reversed for individuals aged 5 years or older, where males contributed more than females to σ_{dg}^2 (Figure 3), reflecting a strong positive covariance between J and b across males in 1 year (Appendix S1). Despite these sex-age class differences, overall male and female contributions to σ_{dg}^2 were similar (means of 0.61 and 0.57 respectively, Figure 3, Appendix S1).

3.4 | Genetic estimates of N_e

Across the 13 microsatellite loci, the number of alleles per locus ranged from two to six and observed and expected heterozygosities ranged from 0.06 to 0.91 and 0.09 to 0.72 respectively (full microsatellite marker summary statistics are provided in Appendix S4).

The single-sample LD method estimated $N_e = 50$ (95% CI: 37–69, using genotypes from 93 individual choughs) given a critical allele frequency of 0.02. N_e estimates were larger (up to 38% larger), with wider 95% CIs, when low frequency alleles were included (Appendix S4). The ABC method estimated $N_e = 26$ (95% CI: 21–36, using genotypes from 71 individual choughs). This estimate was robust to the different upper prior boundaries (Appendix S4).

4 | DISCUSSION

Estimation of effective population size, N_e , and identification of underlying components of demographic variance that reduce N_e below N , is required to understand inter-relations between demography and evolutionary processes (Charlesworth, 2009), and to predict population viability and inform population management strategies (Frankham et al., 2014; Hare et al., 2011; Mace & Lande, 1991). However,

estimating and interpreting N_e for wild populations is extremely challenging, particularly given overlapping generations, environmental and demographic stochasticity and heterogeneity and resulting dynamic age-structure, and given gene-flow stemming from immigration (Caballero, 1994; Wang & Whitlock, 2003; Waples et al., 2011). Such effects could substantially impact N_e but are often ignored (Engen et al., 2005; Engen, Lande et al., 2007), impeding understanding of evolutionary processes and population viability analyses. We used detailed individual- and population-level demographic data to estimate N_e/N , and its underlying components of sex- and age-specific demographic variance, in a small and apparently isolated red-billed chough population, while accounting for environmental and demographic stochasticity by considering reproductive value. Additionally, we used two single-sample genetic estimators of N_e to encompass effects of any unobserved immigration.

4.1 | N_e and demographic variance

Our demographic estimate of N_e/N for Islay's chough population was 0.21. This is substantially lower than the mean value of 0.65 ± 0.15 SD estimated across diverse bird populations, where N_e/N was calculated from mean life-table data assuming constant population size and age-structure and hence no environmental or demographic stochasticity or additional demographic heterogeneity (using the 'AgeNe' estimator, Waples et al., 2013). The low N_e/N in choughs arose because the estimated total demographic variance was relatively high ($\sigma_{dg}^2 = 0.71$) compared to other bird species with similar generation times. Specifically, the female demographic variance component for choughs of $\sigma_d^2 = 0.57$ exceeds the value of $\sigma_d^2 \approx 0.25$ for a generation time of 7 years (extrapolated from Sæther, Engen, Pape Møller et al., 2004). Furthermore, the total σ_{dg}^2 estimated for choughs is notably high for a monogamous species, where reproductive skew might be expected to be relatively small (Sæther, Engen, Lande et al., 2004). This high σ_{dg}^2 is perhaps not surprising since first-year survival is known to vary consistently among nest sites on Islay, creating additional demographic heterogeneity and influencing population dynamics (Reid et al., 2006). Similarly high demographic variance, and small N_e/N , might also arise in other populations where individual reproductive success varies with territory quality (e.g. Griffen & Norelli, 2015; Sergio et al., 2009; Van de Pol, Bruinzeel, Heg, Van Der Jeugd, & Verhulst, 2006). However, commonly used softwares for population viability analysis often assume a Poisson distribution of family sizes (e.g. RAMAS, Akçakaya, 2002; although see VORTEX v.10, Lacy & Pollak, 2014), meaning that demographic variance will be underestimated and N_e/N overestimated (Frankham et al., 2014; Kendall & Wittmann, 2010). Furthermore, our estimate of $N_e = 0.21$ for choughs may itself be a slight overestimate, because the Engen et al. (2010) demographic estimator, like other demographic estimators that consider age-structure (e.g. 'AgeNe', Waples et al., 2011, 2013), assumes zero demographic covariance within individuals across years. For relatively long-lived species that show nest-site and mate fidelity, individual reproductive success might be positively correlated across years (Hamel, Gaillard, Festa-Bianchet, & Côté, 2009; Lee, Engen, & Saether, 2011).

Such persistent individual differences can create additional demographic heterogeneity, which could increase the total variance in lifetime reproductive success and thereby further reduce N_e/N . Indeed, individual reproductive success (b) was moderately repeatable within individuals across years in the focal cough population ($R = .22$, 95% CI: 0.00–0.40, Appendix S1). Future developments of demographic estimators of N_e should aim to incorporate such persistent individual differences alongside other forms of demographic stochasticity and heterogeneity.

4.2 | Causes of demographic variance

A major advantage of estimating N_e/N using demographic estimators that consider age-structure is that such estimators potentially allow each sex and/or age class's contribution to total σ_{dg}^2 , and hence to reducing N_e/N , to be explicitly quantified (Engen et al., 2010; see also Waples et al., 2013). Critical demographic classes that influence N_e , and thereby influence a population's evolutionary trajectory and viability, can then be identified. The detailed demographic data available for Islay's cough population, where survival and any reproduction of adults and sub-adults can be directly observed, and immigration is apparently very rare or absent, provides an unusual and extremely valuable opportunity to partition total demographic variance across key sex-age classes.

Our analyses showed that 4-year-olds and the defined terminal age-class comprising adults aged 5 years or older contributed most to σ_{dg}^2 (Figure 3). This might be expected, since these classes encompass most breeding adults and hence encompass substantial among-individual variation in reproductive success. Overall, male and female contributions to total σ_{dg}^2 were similar (Figure 3). This concurs with the similar sex-specific components of demographic variance (0.16 and 0.14 for females and males respectively) estimated in Siberian jays (*Perisoreus infaustus*), a corvid with a similar life-history to coughts (Engen et al., 2010). However, estimates of sex-specific demographic variances in populations of other bird species have shown larger contributions from males than females (e.g. great reed warbler *Acrocephalus arundinaceus*, Sæther, Engen, Lande et al., 2004; house sparrow, Engen, Ringsby et al., 2007). Further, although total female and male components of σ_{dg}^2 were similar in coughts, the age-specific contributions differed between the sexes. Specifically, ≥ 5 year-old males contributed more to σ_{dg}^2 than ≥ 5 year-old females, whereas two and 3-year-old females contributed more than two and 3-year-old males (Figure 3). Thus, although overall sex-specific components of σ_{dg}^2 were similar, our analyses illustrate that there may be key sex-age-specific processes acting at small population sizes that drive evolutionary processes and population viability, through their influence on N_e . These sex-age specific differences may reflect persistent population or life-history characteristics, or may reflect stochastic demographic processes acting at small population sizes. In general, estimates of N_e from demographic data commonly only consider the female component of demographic variance (Frankham, 1995; Grant & Grant, 1992; Nunney & Elam, 1994; Waples et al., 2013). Our results show that, even for monogamous species like coughts, sex-age-class specific

contributions to demographic variance should be incorporated into calculations of N_e to avoid bias and identify key demographic classes, and hence elucidate potential underlying ecological mechanisms.

4.3 | Genetic and demographic approaches

The demographic estimate of $N_e/N = 0.21$ yielded an estimate of $N_e \approx 30$, given $N \approx 141$. Two different single-sample genetic estimators based on LD and ABC further supported the conclusion that $N_e \leq 50$. Direct quantitative comparison between different N_e estimators is difficult (Robinson & Moyer, 2013), not least because demographic estimators of N_e reflect processes in the offspring generation and estimate N_{ev} (Kimura & Crow, 1963), while single-sample genetic estimators reflect processes in the parental generation and estimate N_{ei} (Crow & Denniston, 1988). Genetic estimates of N_{ei} may therefore lag behind changes in N by at least one generation. Indeed, N_{ei} estimated from LD may be influenced by processes occurring multiple generations previously, as LD can take multiple generations to break down (Wang, 2005; Waples, 2005). Genetic estimators also incorporate effects of immigration and gene flow, which demographic estimators do not (e.g. Baalsrud et al., 2014). However, effects on N_e estimates will depend on the extent of immigration. Immigration of few genetically differentiated individuals could cause N_e to be underestimated, because LD generated by immigration will be attributed to drift. Conversely, high migration rates could cause local population N_e to approach metapopulation N_e (Gilbert & Whitlock, 2015; Wang, 2005; Waples & Do, 2008).

In practice, the LD estimator gave the largest estimate of N_e for Islay's cought population, which may reflect the somewhat larger past population size (e.g. 78 breeding pairs in 1986, Finney & Jardine, 2003; Appendix S2). The ABC estimator gave a similar estimate of N_e to the demographic estimator. Since the ONESAMP ABC approach utilizes multiple different summary statistics to estimate N_e , the exact number of previous generations to which the estimate applies is unclear (Wang, 2009). However, this estimator might be less biased by N_e of previous generations than the LD estimator and may therefore better approximate current N_e in a population of varying N . The alternative explanation that the LD estimator is detecting immigration seems unlikely, as this is not supported by the ABC estimator. Additionally, for the LD approach to give an upwardly biased estimate of N_e there would need to be considerable successful immigration into the Islay population, which is unlikely to have gone unobserved during population monitoring and ringing of all UK cought populations. Thus, there is likely to be little or no immigration and resulting gene flow that might act to increase genetic diversity and N_e in Islay's cought population beyond that calculated from observed N and demography.

4.4 | Conservation management implications

Our insights into the magnitude and demographic causes of N_e/N given dynamic age-structure are also directly relevant to conservation strategy for the focal cought population. The demographic and genetic estimators all showed that $N_e \leq 50$, which is below the rule-of-thumb

minimum recommended to ensure short-term population viability (Frankham et al., 2014; Mace & Lande, 1991). Specifically, the base-line per-generation increase in inbreeding, and the corresponding expected rate of loss of genetic diversity per generation, can be calculated as:

$$\Delta F = \frac{1}{2N_e} \quad (4)$$

(Falconer & Mackay, 1996). From the demographic estimate of $N_e \approx 30$, ΔF will be ≈ 0.02 per initial generation in the continued absence of immigration. This value is relatively high, implying increasing expression of inbreeding depression and reduced evolutionary potential, and hence reduced population viability in both the short-term and long-term (Frankham et al., 2014; Keller & Waller, 2002). Genetic management should therefore be urgently considered. Since the observed high σ_{dg}^2 stems partly from spatial variation in offspring survival to age one (Reid et al., 2006), future strategies could aim to reduce this variation through targeted management of territories with current low productivity (e.g. through targeted habitat improvement or supplementary feeding of specific breeding adults). Additionally, observed sex-age specific contributions to σ_{dg}^2 suggest strategies to alleviate demographic variance could focus on different age classes in females vs. males. However, strategies to decrease σ_{dg}^2 and hence increase N_e/N may be insufficient to ensure future viability of Islay's chough population, as current levels of inbreeding and genetic diversity would not be decreased and increased, respectively. Furthermore, because $\lambda < 1$, N will continue to decrease. Indeed, the low λ may partly reflect inbreeding depression in survival and reproduction (e.g. Liberg et al., 2005; O'Grady et al., 2006). Translocations may consequently be required to re-establish connectivity between Islay and other UK chough populations and thereby increase genetic diversity and ameliorate inbreeding. Re-establishment of gene-flow in small, fragmented populations has been associated with increased fitness and λ ('genetic rescue') in diverse species (Frankham, 2015; Hostetler, Onorato, Jansen, & Oli, 2013; Laikre et al., 2016). Such pro-active genetic management, alongside habitat management, might be essential to ensure long-term population viability.

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AUTHORS' CONTRIBUTIONS

A.E.T. and J.M.R. conceived the ideas and undertook the demographic data analyses; A.E.T. undertook molecular genetic analyses, and S.B.P.

assisted with labwork; E.B., D.McC., J.M.R. and A.E.T. collected field data; A.E.T. wrote the manuscript, assisted by J.M.R.

DATA ACCESSIBILITY

All data associated with this article is available at the Dryad Digital Repository <https://doi.org/10.5061/dryad.68kk0> (Trask, Bignal, McCracken, Piertney, & Reid, 2017).

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